Sensitivity of breeding parameters to food supply in Black-legged Kittiwakes *Rissa tridactyla*

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We fed Herring *Clupea harengus* to pairs of Black-legged Kittiwakes *Rissa tridactyla* throughout the breeding season in two years at a colony in the northern Gulf of Alaska. We measured responses to supplemental feeding in a wide array of breeding parameters to gauge their relative sensitivity to food supply, and thus their potential as indicators of natural foraging conditions. Conventional measures of success (hatching, fledging and overall productivity) were more effective as indicators of food supply than behavioural attributes such as courtship feeding, chick provisioning rates and sibling aggression. However, behaviour such as nest relief during incubation and adult attendance with older chicks were also highly responsive to supplemental food and may be useful for monitoring environmental conditions in studies of shorter duration. On average, the chick-rearing stage contained more sensitive indicators of food availability than prelaying or incubation stages. Overall, rates of hatching and fledging success, and the mean duration of incubation shifts were the most food-sensitive parameters studied.

Seabirds are important indicators of conditions in the marine environment because they are easy to observe during the breeding season and relatively sensitive to fluctuations in prey availability (Cairns 1987, Aebischer *et al.* 1990, Hamer *et al.* 1993). If seabirds are to be used in this manner, however, it is important to identify and monitor the strongest signals of food stress. Mixed views exist on the question of which breeding parameters are most sensitive to food supply. Some authors consider breeding success and chick growth the most food-sensitive parameters (Wehle 1983, Cairns 1987, Baird 1990), whereas others suggest that adult time budgets are better measures (Burger & Piatt 1990, Regehr & Montevecchi 1997, Zador & Piatt 1999).

To use seabirds effectively to assess marine resources, prey availability must be quantified independently so that responses observed in the birds may be calibrated (Burger & Piatt 1990, Monaghan 1996). This is often logistically difficult and expensive, biased by sampling area, or dependent on suboptimal fishery data (Cairns 1987, Navarro 1991). An alternative approach is to provide free-living birds with an unlimited food supply while simultaneously recording a suite of breeding parameters throughout the breeding season. Food supplementation experiments on seabirds have been conducted primarily during the chick-rearing period (e.g. Wehle 1983, Ricklefs *et al.* 1987, Hamer *et al.* 1998). A small number have occurred prior to chick rearing (e.g. Reid 1987, Hiom *et al.* 1991, Hario 1997), while only one has encompassed the entire breeding cycle (Van Klinken 1992). Among responses to supplemental feeding, adult behaviour and activity budgets have been largely neglected, yet those variables are thought to have high potential to reveal food limitation (Cairns 1987, Van Klinken 1992, Monaghan 1996). To date, food supplementation in seabirds has been largely restricted to alcids and ground-nesting larids. Cliff-nesters, because of their inaccessible sites, have not been investigated in this manner.

We present results from a supplemental feeding study of Black-legged Kittiwakes *Rissa tridactyla* (herewith Kittiwake). Kittiwakes are specialists that feed only at the ocean surface and have relatively short foraging ranges away from their breeding sites (Irons 1992, Suryan *et al.* 2000). These features render them particularly vulnerable to prey shortages. We provided Kittiwakes with unlimited food, and compared their breeding performance (egg size, phenology, adult and chick behaviour, parental attendance, chick growth and survival, breeding success) with that of unfed pairs observed concurrently.

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We ranked breeding parameters according to the magnitude of change induced by supplemental feeding to determine their value as indicators of food availability. Our approach differed from other supplemental feeding studies in that we: (1) provided food to free-ranging adults and their young, (2) provided food *ad libitum* through the entire breeding season, (3) measured a large number of responses considered likely indicators of nutritional status and (4) identified and ranked the breeding parameters most affected by food availability.

METHODS

Study area

The study was conducted on Middleton Island, Alaska, which lies 120 km from the mainland coast in the northern Gulf of Alaska (59°26′N, 146°20′W). The island measures about 2 × 8 km and has several kilometres of low (10–30 m) cliffs along its perimeter that are used extensively for nesting by about 20 000 pairs of Kittiwakes. Birds also nest on several artificial structures on Middleton, including the dilapidated buildings of an abandoned U.S. Air Force facility decommissioned in 1963. We sampled Kittiwakes nesting on the largest of several radar towers at the Air Force site. Various enhancements were made to this tower to encourage use by Kittiwakes and to aid observation and manipulation of nesting and feeding activity.

Supplemental feeding

In 1994–1995, we installed 144 wooden nest platforms (24 × 35 cm) on the upper walls of the 12-sided polygonal-shaped tower, about 10–13 m above ground level. Each nest site was fitted with a sliding pane (26 × 30 cm) of one-way mirror glass and a small food tray (5-cm-diameter plastic pipe cut lengthways) that passed through a plywood wall.

In 1996 and 1997, we provided supplemental food (thawed herring *Clupea harengus*) to Kittiwakes in selected sites on the tower. Feeding occurred two or three times daily from 9 May (about 3 weeks before first laying) to 16 August in both years. Food was offered at 09:00 and 17:00, and the quantity consumed and left uneaten per pair was monitored by weighing the fish remaining after each feeding averaged over all study nests. In 1997, we added a midday feeding (13:00) when 2-week-old chicks began to eat from the trays.

To investigate the seasonality of food shortages, we established three treatment groups of pairs that received food from the beginning of observations (9 May) through: (1) completion of the clutch ('fed-to-laying' group; 26 pairs in 1996, 27 pairs in 1997), (2) completion of hatching ('fed-to-hatching' group; 26 pairs both years) and (3) fledging of young ('fed-all-season'; 27 pairs in 1996, 25 pairs in 1997). Control (unfed) samples included 63 pairs in 1996 and 65 pairs in 1997. We found no evidence that birds whose food was discontinued benefited from having been fed earlier in the same season (Gill 1999). Thus, pairs that were no longer being fed were added to the control group for comparison with birds still being fed at later stages.

Pairs in the three fed groups and the control sites were clustered, each treatment occupying one to one and a half walls of the tower. Although a random dispersion of treatment types among panels might have increased the independence of sample units, the potential for food stealing among neighbouring pairs might effectively have eliminated our treatment groups. The clustered design essentially eliminated any food stealing. The six walls used in the experiment were located on the same (west) side of the tower, occupying only 22 m of linear wall space. The artificial nature of the nest sites ensured that habitat quality was uniform across all treatments. The two extreme treatment groups (control and fed-all-season) were on adjacent walls. For those reasons, sites were treated as independent sample units in the analysis.

Herring were cut into ingestible pieces before presentation to the birds. Vitamin B1 (thiamine) was added to offset losses of that nutrient associated with freezing (Crissey 1998). Food consumption approximated to the total food requirements calculated in other studies (Gabrielsen *et al.* 1987, 1992, Gill 1999). Thus, comparisons of behaviour and breeding performance made between fed and unfed groups appear to reflect Kittiwakes whose food requirements were completely met contrasted with those limited by natural food sources.

Measurement of behaviour

The removable one-way glass windows installed behind nests permitted close observation of breeding activity and the capture of adults and young as needed for marking and measurements. We monitored 142 and 143 window sites in 1996 and 1997, respectively. Adults and chicks were marked with a U.S. Fish and Wildlife Service (USFWS) metal ring

and plastic colour rings. In both years, all nest sites were checked twice daily to record the timing of laying, hatching, fledging and mortality. Adults were sexed by behaviour, genetics or morphometrics (Jodice *et al.* 2000).

We monitored behaviour of adults and chicks using continuous (all occurrences) sampling (Altmann 1974) and expressed rates as the number of 5-min intervals per hour during which a focal behaviour occurred. During courtship and chick-rearing watches, equal numbers of fed and unfed pairs were observed simultaneously and continuously from 07:00 to 09:00 and from 15:00 to 17:00. Attendance patterns were monitored by recording the number of site owners present at the beginning of each 5-min interval. All observations were made from inside the tower at distances of 2–3 m.

Observations during courtship totalled 1460 nest-hours from 21 May to 8 June 1996 and 1477 nest-hours from 25 May to 10 June 1997. In total, 27 fed and 13 unfed pairs were included in the court-ship study in 1996, whereas 53 fed and 21 unfed pairs were observed in 1997. Variables recorded included female begging towards her mate, court-ship feeding (scored only if food was passed from male to female), copulation and number of adults present.

In 1996, incubation shift changes were monitored daily using spot-checks for male or female presence every 2 h from 09:00 to 19:00. Observations began on day 4 of incubation and continued until the first egg hatched or all eggs were lost.

Behaviour observations during chick rearing totalled 750 nest-hours from 7 July to 26 July 1996 and 2028 nest-hours from 1 July to 16 August 1997. Totals of 13 fed and 12 unfed sites were included in the chick behaviour study in 1996, whereas 16 fed and 28 unfed sites were observed in 1997. Observations of a site began when the first chick hatched, and concluded once all chicks died or reached 40 days of age. In two-chick broods, the identity of the chick exhibiting each behaviour was noted (based on picric acid marks on the head of the first hatched *a*-chick). At each nest site, we recorded chick begging bouts, chick feeding (i.e. food passed from parent to chick), aggressive interactions between siblings (defined as pecks or bill jabs by a chick toward its sibling) and the number of adults present. Data on sibling aggression and begging rates were not collected in 1996. To ensure adequate sample sizes, we added new nests when chicks in previously sampled nests perished.

Breeding performance

Egg volume was estimated from measures of length and breadth, using published formulae (Coulson 1963). Egg order was recorded in 1997 only. Meas-urements were taken to the nearest 0.1 mm with vernier callipers. Chicks were weighed and meas-ured every 5 days from hatching until 40 days of age. Body mass was measured to ± 1 g using an electronic balance for smaller chicks and a Pesola® spring scale for larger chicks. In 1997, wing chord (±1 mm) was measured using a wing-rule. Age at fledging (first observed flight) was recorded for each chick, although for survival analyses chicks were considered to have fledged at 40 days of age.

Data analysis

Breeding parameters measured in this study focused on three distinct stages of the nesting cycle. In most cases, we predicted the direction of change that would occur under supplemental feeding, but in some instances we could not (Appendix 1). We tested the null hypothesis that there were no differences in mean performance between fed and unfed Kittiwakes for all breeding parameters measured. Rejection levels were set at $P = 0.05$ (two-tailed tests). Results are presented as mean ± se throughout the paper. Non-parametric statistical tests were used when the variables being analysed did not meet the assump-tions of normality or homogeneity of variances.

We subdivided courtship behaviour into three intervals for analysis based on temporal trends in behaviour frequencies. These included 19–11 days before egg laying, the 10 days prior to egg laying, and the 7 days following appearance of the first egg. Due to earlier laying in the fed group in 1997, we had inadequate data for the 19–11 days before laying period analysis.

The average length of an incubation shift was esti-mated as the reciprocal of the mean number of shift changes per hour (Hamer *et al.* 1993). Observations during chick rearing were divided into early chick rearing (0–20 days) and late chick rearing (21–40 days), and rates for all behaviour were calculated per nest or pair to minimize the possibility of non-independence of the observations. Adult attendance was quantified by the percentage of adults present (100% = both, 50% = one adult) at each 5-min mark. Adult attendance during courtship and chick rearing was summarized using the intervals described above. Because attendance was measured in percentages,

Table 1. Prelaying and immediate post-laying behaviour of fed and unfed Black-legged Kittiwakes on Middleton Island, 1996–97.[a]

Behaviour	Period (days)[b]	1996			1997		
		Fed	Unfed	P	Fed	Unfed	P
Attendance[c]	−19 to −11	70.4 ± 5.6 (11)	72.5 ± 3.9 (10)	0.852	–	–	–
•	10 to 0	65.5 ± 1.9 (27)	66.2 ± 2.4 (13)	0.886	59.8 ± 1.0 (53)	68.5 ± 2.0 (21)	**< 0.001**
	1 to 7	52.8 ± 0.9 (8)	53.8 ± 0.9 (10)	0.476	51.9 ± 0.4 (52)	58.7 ± 2.9 (16)	**< 0.001**
Courtship begging[d]	−19 to −11	0.11 ± 0.05 (11)	0.12 ± 0.04 (10)	0.744	–	–	–
•	10 to 0	0.43 ± 0.05 (27)	0.29 ± 0.04 (13)	0.075	0.47 ± 0.06 (53)	0.70 ± 0.09 (21)	**0.015**
	1 to 7	0.12 ± 0.06 (8)	0.06 ± 0.02 (10)	0.807	0.03 ± 0.01 (52)	0.13 ± 0.06 (16)	**0.007**
Courtship feeding[d]	−19 to 11	0.06 ± 0.03 (11)	0.09 ± 0.03 (10)	0.295	–	–	–
•	10 to 0	0.31 ± 0.04 (27)	0.16 ± 0.02 (13)	0.007	0.16 ± 0.03 (53)	0.12 ± 0.05 (21)	0.392
	1 to 7	0.04 ± 0.02 (8)	0.03 ± 0.01 (10)	0.629	0.01 ± 0.01 (52)	0.04 ± 0.02 (16)	0.091
Copulation[d]	−19 to 11	0.03 ± 0.02 (11)	0.02 ± 0.01 (10)	0.376	–	–	–
•	10−0	0.08 ± 0.01 (27)	0.09 ± 0.02 (13)	0.695	0.10 ± 0.02 (53)	0.14 ± 0.03 (21)	**0.036**
	1 to 7	0.01 ± 0.01 (8)	0.00 ± 0.00 (10)	0.264	0.01 ± 0.01 (52)	0.02 ± 0.02 (16)	0.361

[a]All units are occurrences per pair per hour (mean ± se, *n* of pairs in parentheses). *P* < 0.05 in bold type.
[b]Appearance of first egg in clutch is day 0.
[c]Attendance expressed as percentage; 100% indicates both adults present at every observation. Two-tailed *t*-statistics calculated on arcsine transformed values.
[d]Within-year differences between groups tested using Mann–Whitney *U*.

we arcsine-transformed the data prior to analysis. For each fed and unfed chick, growth in body weight between days 5 and 25, and wing chord between 10 and 30 days were computed by linear regression. Differences between treatment groups in the measured parameters were analysed with the Student *t*-test or Mann–Whitney *U* statistic. We used the Kaplan–Meier survival estimator to test for differences in chick survival between treatment groups with a log-rank chi-square test (Steinberg *et al.* 1997). Within treatments, no significant differences were found in growth or survival between single-chick broods and *a*-chicks, so these samples were combined for subsequent analyses.

To provide a standardized measure of sensitivity to food supply for each variable (65 in total, see Appendix 2), we expressed the response to supplemental feeding (effect size) in standard deviations using the formula: effect size = $(x_\text{fed} - x_\text{unfed})/\text{sd}_\text{unfed}$. Effect size was expected to be a positive or negative value depending on the predicted response to supplemental feeding for a given measurement (i.e. fed > unfed or fed < unfed; Appendix 1). We determined the mean size of the effect for variables measured in both years because Spearman rank correlation indicated a positive relationship. We then took the absolute values of single-year or mean effect sizes and ranked all parameters relative to one another. A high rank indicated that a variable was strongly affected by food supplementation.

RESULTS

Prelaying and egg production

Attendance dropped steadily in the prelaying period, until at clutch completion only one adult was present (Table 1). In both treatment groups and years, courtship begging, courtship feeding, and copulation peaked in the last 10 days before the first egg appeared in a clutch. Unfed females begged at significantly greater rates than fed females in 1997, but received food from their mates at similar rates. Begging rates of unfed and fed females were similar in 1996, yet unfed females received less food from their mates than fed females. While copulation rates were the same in fed and unfed pairs in 1996, unfed pairs copulated at significantly higher rates than fed pairs in 1997. Prior to laying, fed pairs attended their nest sites at similar rates to unfed pairs in 1997 but at significantly lower rates in 1996.

On average, eggs laid by fed females were similar in volume to those laid by unfed females ($t_{228} = -0.56, P = 0.577$ in 1996, $t_{229} = 1.62, P = 0.107$ in 1997). However, laying sequence and clutch size affected that response. *A*-eggs were larger in volume than *b*-eggs regardless of treatment group (Fig. 1). Although we found no difference between treatment groups in the volume of *a*-eggs ($t_{96} = 0.97, P = 0.334$; analysis limited to 1997 data), the volume of single eggs laid by fed females was 7% smaller than those
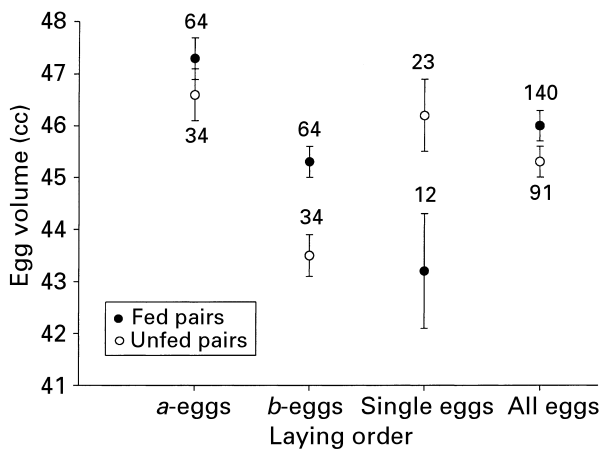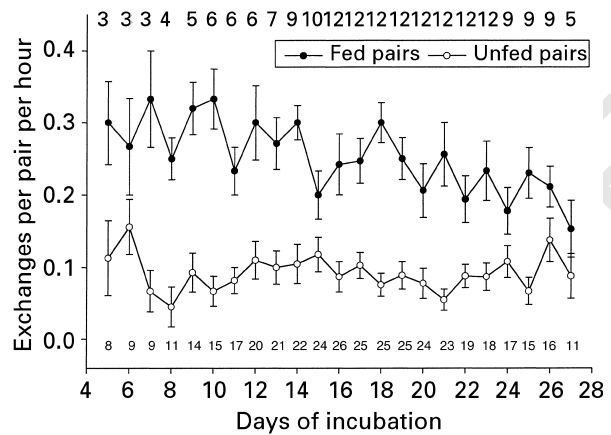
Figure 1. Egg volumes (mean ± se) in relation to laying order in fed and unfed pairs of Black-legged Kittiwakes on Middleton Island in 1997.

Figure 2. Hourly exchange rate (mean ± se) of fed and unfed pairs of Black-legged Kittiwakes during incubation on Middleton Island, 1996. Sample sizes of fed and unfed pairs shown on top and bottom axes, respectively.

from unfed females ($t_{33} = -2.41$, $P = 0.022$). The volume of single eggs was smaller than a-eggs in the fed group ($t_{74} = 3.81$, $P < 0.001$), but not in the unfed group ($t_{55} = 0.54$, $P = 0.591$). B-eggs were 4% larger when laid by fed females compared to those laid by unfed females ($t_{96} = 3.48$, $P < 0.001$).

Incubation

Fed females laid their first egg significantly earlier (3–4 days) than unfed females (Table 2). There was no difference, however, in the time it took to complete two-egg clutches; both treatment groups had a mean interval of about 2.5 days between eggs. Incubation time did not differ between fed and unfed

pairs; the mean incubation period was 27 days in both years (Table 2).

The number of shift changes per pair per hour during incubation was higher in fed pairs than in unfed pairs ($U_1 = 323$, $P < 0.001$; Fig. 2). On average, unfed pairs had incubation shifts 2.5 times longer than those of fed pairs (10.6 h vs. 4.2 h).

Chick rearing

Fed pairs hatched their first egg 3–4 days earlier than unfed pairs in 1996 and 1997 (Table 2). Within-clutch synchrony of hatching was similar for fed and unfed broods in both years (Table 2).

Table 2. Laying and hatching dates, laying and hatching synchrony, and incubation period (mean ± se, *n* of pairs) of fed and unfed Black-legged Kittiwakes on Middleton Island, 1996–97.

Year	Treatment	Laying		Hatching		Incubation (days)[c,d]
		Mean date[a,d]	Within-clutch synchrony (days)[b,e]	Mean date[a,d]	Within-clutch synchrony (days)[b,e]	
1996	Fed	4 June ± 0.6 (73)	2.5 ± 0.1 (67)	1 July ± 0.6 (54)	1.8 ± 0.2 (44)	27.7 ± 0.2 (34)
	Unfed	7 June ± 0.7 (59)	2.6 ± 0.1 (48)	4 July ± 0.7 (43)	1.2 ± 0.1 (32)	27.5 ± 0.2 (46)
	P	**< 0.001**	0.537	**0.007**	0.068	0.443
1997	Fed	3 June ± 0.5 (77)	2.2 ± 0.1 (64)	30 June ± 0.4 (55)	1.5 ± 0.1 (37)	27.6 ± 0.2 (36)
	Unfed	7 June ± 0.4 (59)	2.4 ± 0.1 (35)	4 July ± 0.5 (32)	1.5 ± 0.2 (15)	27.2 ± 0.2 (41)
	P	**< 0.001**	0.244	**0.001**	0.788	0.225

[a]Mean laying and hatching dates of first-laid and first-hatched egg per clutch.
[b]Mean intervals between first and second eggs (laying or hatching) in 2-egg clutches.
[c]Interval from first-laid to first-hatched egg in a clutch.
[d]Within-year differences tested using *t*-distribution (2-tailed); *P* < 0.05 in bold type.
[e]Within-year differences tested using Mann–Whitney *U* statistic (2-tailed); *P* < 0.05 in bold type.

Table 3. Effects of treatment group and hatching order on Kittiwake growth parameters, Middleton Island, 1996–1997: statistical significance of pairwise contrasts.

| | | Treatment (fed vs. unfed)[a] | | | | | | Hatching order (*a*- vs. *b*-chicks)[a] | | | | | |
| | | *a*-chicks | | | *b*-chicks | | | Fed chicks | | | Unfed chicks | | |
Parameter	Year	*t*	*df*	*P*	*t*	*df*	*P*	*t*	*df*	*P*	*t*	*df*	*P*
Hatching mass	1996	0.34	93	0.733	0.30	69	0.768	1.49	35	0.146	2.69	127	**0.008**
	1997	0.48	85	0.633	1.36	50	0.180	0.24	30	0.809	2.14	105	0.035
Weight gain	1996	3.98	80	**< 0.001**	3.17	36	**0.003**	1.40	32	0.172	3.88	84	**< 0.001**
	1997	5.07	70	**< 0.001**	4.84	26	**< 0.001**	0.59	26	0.558	3.44	70	**0.001**
Peak mass	1996	4.95	77	**< 0.001**	4.41	29	**< 0.001**	2.54	31	**0.016**	4.24	75	**< 0.001**
	1997	2.53	63	**0.014**	2.49	19	**0.022**	0.51	25	0.615	2.08	57	0.057
Age at peak mass	1996	−1.08	77	0.285	0.35	29	0.732	0.70	31	0.491	2.12	75	**0.038**
	1997	−1.90	63	0.061	−1.07	19	0.298	−0.98	25	0.337	−1.059	57	0.294
Wing chord	1997	2.33	69	**0.023**	2.50	25	**0.019**	0.18	26	0.862	3.83	68	**< 0.001**
Age at fledging	1996	−1.38	47	0.175	−1.24	14	0.237	0.27	23	0.782	−0.43	38	0.672
	1997	−0.98	40	0.335	0.38	7	0.718	−0.33	17	0.741	0.67	30	0.511

[a]$P < 0.05$ in bold type.
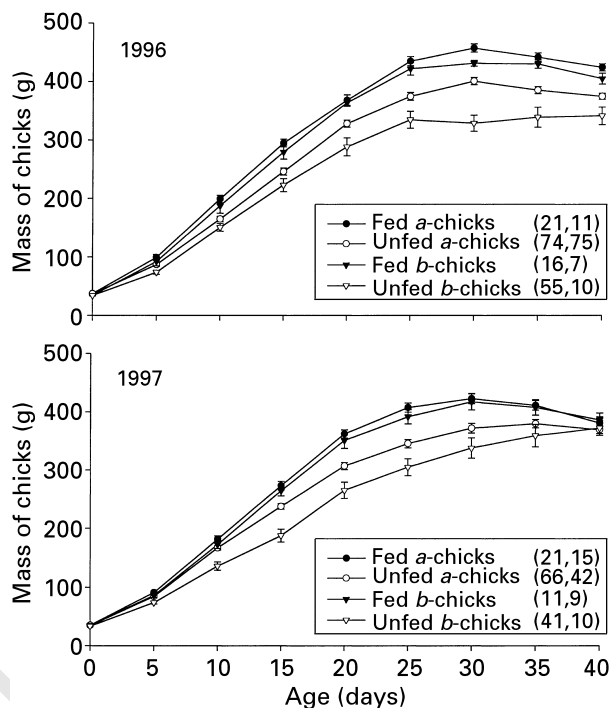
Figure 3. Weight gain (mean ± se) of Black-legged Kittiwake nestlings relative to age, hatching order and feeding treatment on Middleton Island, 1996–97. Sample sizes at hatching and fledging, respectively, are shown in parentheses. Weight of adults (sexes combined) on Middleton during this study was 403.4 ± 1.8 g ($n = 529$).
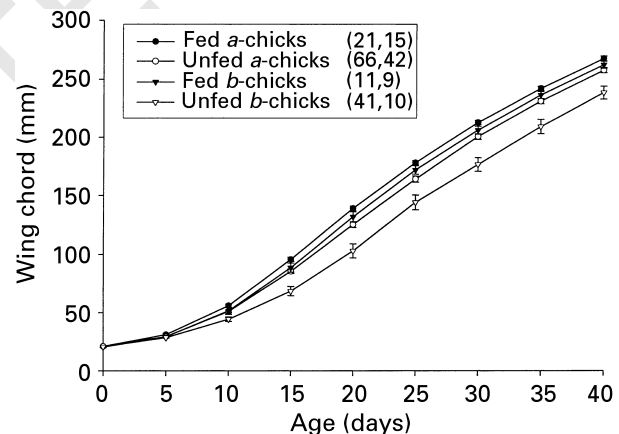
Figure 4. Wing chord (mean ± se) of Black-legged Kittiwake nestlings relative to age, hatching order and feeding treatment on Middleton Island in 1997. Sample sizes at hatching and fledging, respectively, are shown in parentheses.

Whereas unfed *a*-chicks were heavier than their younger siblings at hatching, supplemental food eliminated the difference in hatching weight of siblings within fed broods (Table 3, Appendix 3). Supplemental food had little influence on age at peak mass (averaging 31 days) or age at fledging (averaging 42.5 days). In both years, however, fed *a*- and *b*-chicks attained heavier peak weights than did either unfed *a*- or *b*-chicks.

Weight gain (Fig. 3) and wing chord (Fig. 4) were greater at nests with supplemental food, although
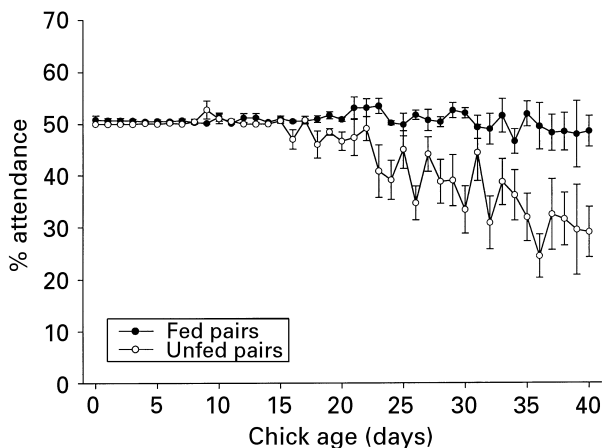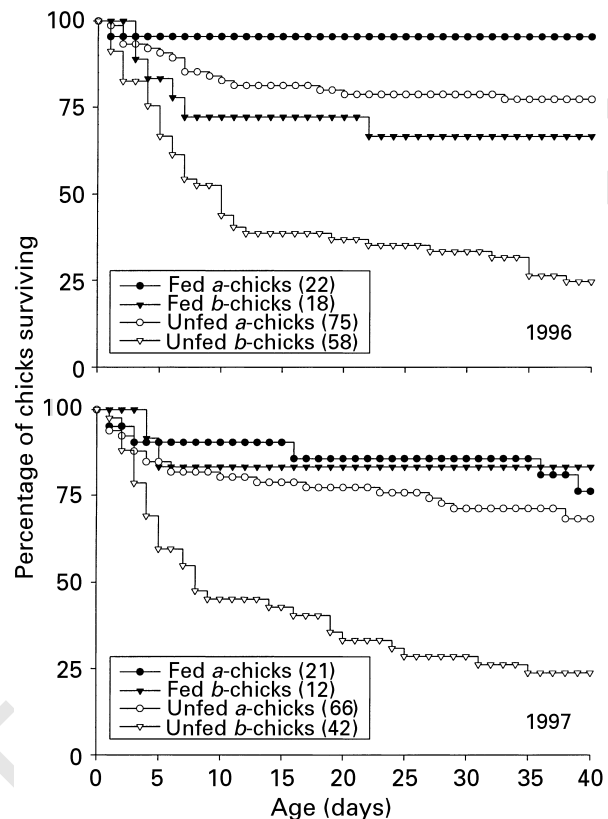
Figure 5. Nest attendance (mean ± se) of fed and unfed Black-legged Kittiwakes during chick rearing on Middleton Island in 1997. Continual presence of both adults at a nest constitutes 100% attendance. Sample sizes of fed and unfed pairs are shown on top and bottom axes, respectively.


Figure 6. Percentage survival of Black-legged Kittiwake chicks in relation to hatching order and feeding treatment on Middleton Island, 1996–97. Single chicks were combined with *a*-chicks because no differences were detected in survival. Sample sizes at hatching are given in parentheses.

wing development was less sensitive than body mass. Feeding eliminated differences in growth between *a*- and *b*-chicks, but *a*-chicks grew significantly faster than *b*-chicks in unfed broods (Table 3). Fed *a*- and *b*-chicks grew significantly faster than their unfed counterparts. Fed chicks fledged at heavier weights in 1996 but at similar weights to unfed chicks in 1997 (Fig. 3). Overall, fed and unfed chicks in 1996 hatched at heavier weights, grew faster, reached heavier peak weights at a younger age, and fledged earlier than their counterparts in 1997 (Appendix 3).

During the first 2 weeks of chick rearing, fed and unfed pairs both guarded their chicks continuously ($t_{42} = 0.85$, $P = 0.399$; Fig. 5; no data available for 1996). After day 16, however, unfed pairs decreased their nest attendance significantly compared to fed pairs (unfed; 39.5%; fed 50.6%; $t_{34} = 4.84$, $P < 0.001$). By fledging, mean attendance per site for unfed pairs was 29.0%, in contrast to 48.5% for fed pairs.

Unfed chicks survived less well than fed chicks ($\chi^2_1 = 8.17$, $P = 0.004$ in 1996, $\chi^2_1 = 7.36$, $P = 0.007$ in 1997), although hatching sequence significantly affected that response. Survival of unfed *b*-chicks (24% in both years; Fig. 6) was significantly lower than that of unfed *a*-chicks and fed *a*- or *b*-chicks (all *P* values = 0.009). Mortality rates were similar among fed and unfed *a*-chicks and fed *b*-chicks in both years.

Supplemental food did not appear to reduce sibling aggression significantly. Fed *a*-chicks exhibited slightly higher rates of aggression toward their younger nest mates relative to unfed *a*-chicks during the first half of chick rearing, but exhibited lower levels thereafter (Fig. 7a).

Food begging increased throughout chick rearing among unfed chicks but decreased in fed chicks (Fig. 7b). However, the rate at which adults fed chicks decreased during chick rearing at both fed and unfed sites (Fig. 7c). Despite these patterns, few significant differences were found. Single chicks in fed sites begged at significantly lower rates than their unfed counterparts during the second half of chick rearing but received significantly more feeds per hour than unfed single chicks during the first half.

Breeding success

Values of laying success, hatching success and chick production for each treatment group are summarized in Table 4. Overall productivity differed markedly between treatment groups. Larger clutches,
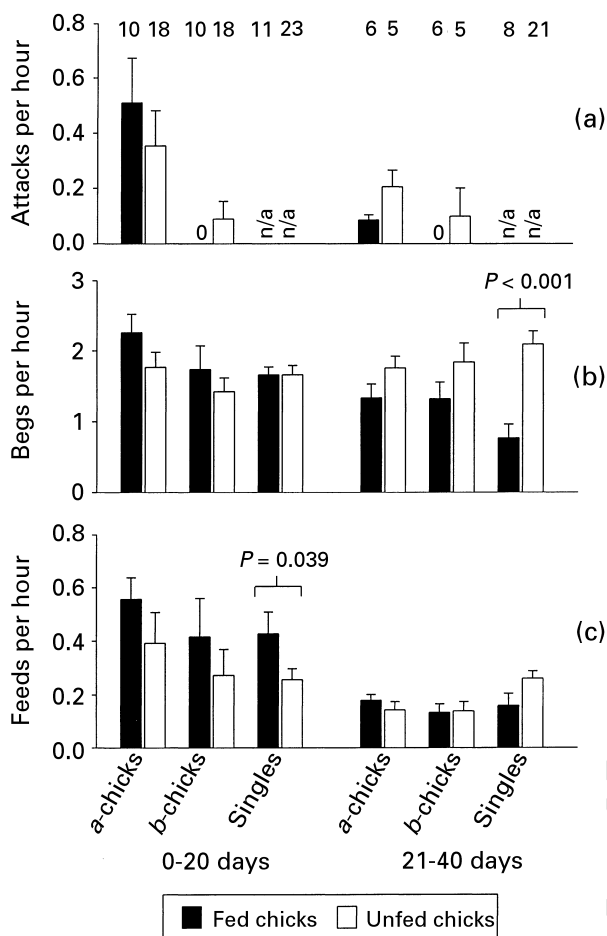
Figure 7. Rates (mean ± se) of: (a) sibling aggression, (b) begging and (c) parental feeding of fed and unfed Black-legged Kittiwake chicks during the first and second halves of the nestling period on Middleton Island in 1997. Sample sizes are displayed along the top axis. Differences between adjacent means (fed vs. unfed) were not significant except as indicated (Mann–Whitney *U*-test).

and higher hatching and fledging success all contributed to the higher productivity of fed Kittiwakes compared to unfed pairs. Laying success was not affected by supplemental feeding in either year. Details concerning the components of productivity will be presented in a forthcoming paper.

Parameters ranked by sensitivity to food

The most sensitive indicators of food availability were (in descending order) fledging success, hatching success, incubation shift length, begging rates of single chicks, adult attendance in the second half of chick rearing, *b*-chick growth and overall productivity (Table 5, Appendix 2). Supplemental feeding improved fledging success of fed pairs by 6–8 standard deviations over unfed pairs and hatching success was enhanced by 2.5–6 standard deviations. The least food-sensitive parameters were generally improved by 0.5 standard deviations or less (Appendix 2).

The chick-rearing stage contained more sensitive indicators of food availability than prelaying and incubation stages, with six of the 10 most sensitive categories of response occurring after hatching (Table 5). The most sensitive measures of food supply were courtship feeding, hatching success, and fledging success during the pre-egg laying, incubation, and chick-rearing stages, respectively.

DISCUSSION

Conventional parameters for monitoring the breeding performance of colonial seabirds (e.g. hatching success, fledging success and overall productivity)

Table 4. Reproductive success of Black-legged Kittiwakes relative to feeding treatment on Middleton Island, 1996–97.[a,b]

	1996		1997	
Parameter[c]	Fed	Unfed	Fed	Unfed
Laying success	0.92 (79)	0.94 (63)	0.97 (78)	0.91 (65)
Clutch size	1.93 (73)	1.85 (59)	1.83 (76)	1.63 (59)
Hatching success	0.76 (49)	0.65 (83)	0.74 (50)	0.50 (85)
Fledging success	0.85 (22)	0.53 (75)	0.81 (21)	0.51 (66)
Breeding productivity	1.32 (25)	0.66 (59)	1.04 (25)	0.37 (59)
Overall productivity	1.26 (27)	0.62 (63)	1.04 (25)	0.34 (65)

[a]For details see Gill (1999).
[b]Mean values; samples size (pairs) in parentheses.
[c]Laying success = nests with eggs/sites with pairs; clutch size = eggs laid/nests with eggs; hatching success = eggs hatched/eggs laid; fledging success = chicks fledged/eggs hatched; breeding productivity = chicks fledged/nests with eggs; overall productivity = chicks fledged/sites with pairs.

Table 5. Ten measures of breeding performance most sensitive to supplemental feeding in Black-legged Kittiwakes on Middleton Island, 1996–1997.

Parameter	Mean effect size (sd's)[a]	Breeding stage
Fledging success[b]	6.41	Chick rearing
Hatching success	4.19	Incubation
Incubation shift length	4.14[c]	Incubation
Chick begging, single chick, day 21–40	1.57[c]	Chick rearing
Adult attendance, day 15–40	1.49[c]	Chick rearing
Weight gain, *b*-chick	1.37	Chick rearing
Fledglings/nest with eggs	1.25	All season
Fledglings/site with pair	1.19	All season
Peak weight, *b*-chick	1.15	Chick rearing
Weight gain, *a*-chick	1.12	Chick rearing

[a]Effect size is the response of breeding parameters to supplemental feeding expressed in standard deviations: $(x_{fed} - x_{unfed})/sd_{unfed}$.
[b]Combines *a*-chicks, *b*-chicks, and single chicks with mean effect sizes of 2.43, 8.23 and 1.30 standard deviations, respectively (Appendix 2).
[c]Parameter measured in one year only.

were the most sensitive indicators of food supply in our study. This is not surprising, as each of these parameters is a cumulative measure of processes and outcomes that occurred over all or a large part of the breeding season. However, some non-conventional measures were also reliable indicators of foraging conditions. In particular, measures of time allocation by adults responded strongly to supplemental feeding. Such measures may be valuable for indicating environmental conditions at specific periods during the breeding cycle. These parameters can be estimated adequately in short (< 1 week) visits to a colony.

Our data suggest that food availability in the ocean was better in 1996 than in 1997. Components of productivity (Table 4), patterns of adult behaviour (Table 1) and chick growth (Appendix 3) were depressed in the latter year, even among fed birds (see also Gill 1999). This suggests that Kittiwake pairs primarily depended on natural food despite food provisioning at the nest. Such differences in natural food availability may have lessened our ability to quantify food sensitivity in 1996.

Responses to supplemental feeding generally followed our predictions. Exceptions included adult attendance before laying, and sibling aggression. Those anomalies and other comparative aspects of our results are addressed below.

Prelaying and egg production

Adult courtship behaviour

Courtship feeding may be energetically important to female larids during egg formation (Chardine 1987, Salzer & Larkin 1990, Neuman *et al.* 1998). Indeed, for both fed and unfed Kittiwakes, the frequency of courtship begging and feeding peaked during egg development (–10 to 0 days). However, the influence of supplemental food on courtship begging and feeding was inconsistent. In 1997, unfed females begged at a significantly greater rate than fed females but both groups received food from their mates at similar rates. In 1996, begging rates were similar, although unfed females received significantly fewer offerings from their mates than fed females. Despite these ambiguous findings, courtship feeding during the egg formation period does appear to be biologically significant in gauging food availability. It was the 15th most sensitive parameter to supplemental feeding among the 65 examined (Appendix 2). On the other hand, female begging was one of the least sensitive variables measured during this study (ranking 50th).

Attendance

The higher nest-site attendance by unfed pairs compared with fed pairs in 1997 (but not in 1996) was surprising given that a previous study had indicated that poor feeding conditions desynchronize pair activities in Herring Gulls *Larus argentatus* (Bukacińska *et al.* 1996). Why fed pairs attended less is difficult to answer but perhaps there is an advantage for well-fed birds early in the season to decrease nest attendance, allowing them to prospect for future feeding areas or engage in other extra-nest activities. Alternatively, Kittiwakes nesting on good quality sites like the tower may face high levels of aggression from prospectors (Porter 1990), forcing poorer quality Kittiwakes (i.e. unfed pairs) to attend their nests at higher rates to avoid losing their site.

Timing of breeding

It is often suggested that early breeding in seabirds indicates good environmental conditions, superior individual quality or both (Coulson 1968, Perrins 1970, Monaghan *et al.* 1989). In our study, eggs were laid 3–4 days earlier in fed pairs than unfed pairs, suggesting that females began egg laying as soon as they were energetically capable of forming eggs (Perrins 1970, Hatch & Hatch 1990). Our results do not support the view that egg laying is

timed so that chick rearing coincides with the period of maximum food availability (e.g. Lack 1968, Nager & Noordwijk 1995). In that case, treatment and control birds would be expected to lay on the same schedule, as laying presumably would be regulated by an environmental cue such as photoperiod (Parsons 1975). Relative to other parameters measured, clutch initiation showed a strong response to food supplementation, ranking 18th out of 65 parameters.

Egg and clutch sizes

Like other supplemental feeding experiments in larids (Reid 1987, Hiom *et al.* 1991, Hario 1997), we found a positive correlation between food supply and egg size. The food effect was only apparent in the *b*-egg, however, with *b*-eggs from fed nests averaging significantly larger than the *b*-eggs from unfed nests. *B*-eggs were, nonetheless, smaller than *a*-eggs in both fed and unfed nests, suggesting that the reduced size of the *b*-egg is adaptive (Bolton *et al.* 1992).

Unexpectedly, fed females laid smaller eggs in single-egg clutches than unfed females. The reason for this is unclear, although the difference in laying success between fed and unfed pairs in 1997 (97% vs. 91%) might be a reflection of poor quality or younger females being induced to breed by food supplementation. Such females might have produced smaller eggs in their single-egg clutches than those laid by better quality females in the unfed group which might have laid a second egg if fed.

Clutch-size showed a weaker response to food supply than egg-size differences. Although fed pairs laid slightly larger clutches than unfed pairs in both years, the difference was significant only in 1997 (Gill 1999). *B*-egg size appears to be a better indicator of food availability (ranking 22nd in the sensitivity analysis) than either the size of *a*-eggs (ranking 52nd) or clutch size (ranking 44th). This agrees with other studies that found egg size to be a more sensitive measure of nutritional status than clutch size (Martin 1987, Hario 1997), and the last egg in a clutch to be the most responsive to food supplies (Houston *et al.* 1983, Reid 1987, Hiom *et al.* 1991).

Incubation

Shift length

Observational studies indicate that Kittiwakes shorten their incubation shifts in response to favourable feeding conditions (Roberts 1988, Hamer *et al.* 1993). Our experimental results support that finding. Fed Kittiwakes alternated incubation duties 2–3 times more frequently than unfed pairs, making shift length the most responsive parameter to food provisioning after fledging and hatching success. Exchange rates in fed and unfed pairs were comparable to Kittiwakes in Shetland during years of abundant food and poor food, respectively (Hamer *et al.* 1993).

Chick rearing

Adult attendance

The lower attendance by unfed pairs during late brood rearing (> 15 days) is consistent with supplemental feeding studies in other seabirds (Hill & Hamer 1994, Bukaciński *et al.* 1998). Our results also support a number of observational studies of Kittiwakes documenting lower adult attendance in food-stressed colonies (Coulson & Johnson 1993, Hamer *et al.* 1993, Roberts & Hatch 1993). The high attendance of both fed and unfed adult Kittiwakes during early chick rearing may reflect the chicks' need for constant brooding and their relatively low food requirement (Coulson & Porter 1985, Gabrielsen *et al.* 1992, Hill & Hamer 1994). After about 2 weeks, however, chicks no longer need constant brooding, and their food requirements increase rapidly. The first factor allows, and the second requires, unfed adults to spend more time foraging.

Adult time budgets have been proposed as perhaps the single most sensitive measure of food supply in both surface-feeding and diving seabirds (Burger & Piatt 1990, Hatch 1990, Monaghan 1996). This is because increased foraging effort helps to minimize detrimental effects on feeding rates, chick growth and survival (Burger & Piatt 1990, Uttley *et al.* 1994, Monaghan 1996). Indeed, this study revealed that adult attendance in the later chick-rearing period as highly sensitive to food conditions (ranking 7th). However, increased foraging effort apparently was not enough to offset poor feeding conditions because chick survival was a more sensitive bio-indicator (ranking 1st) than adult attendance.

Chick growth

Numerous studies have reported that seabird nestling growth is highly responsive to natural foraging conditions (e.g. Monaghan *et al.* 1989, Hamer *et al.* 1991, Barrett & Rikardsen 1992). In this study, daily growth rates and peak weights of both *a*- and *b*-chicks ranked among the top 20 most sensitive parameters measured. Indeed, food supplementation essentially eliminated the differences in growth rates between *a*- and *b*-siblings.

Fledging age and weight

Fledging age did not differ between treatment groups (see also Hudson 1979, Navarro 1991), and was consistent with the average from other studies of Black-legged Kittiwakes (Baird 1994). This is in contrast to other seabird provisioning studies that indicated that fed chicks fledge earlier than unfed chicks (Harfenist 1995, Wernham & Bryant 1998). Fledging weight was higher among fed chicks only in 1996, which was surprising given the evidence that natural food conditions were relatively poorer in 1997. Despite fed and unfed chicks fledging at similar weights in 1997, fed chicks attained higher peak weights and lost weight prior to fledging (as opposed to unfed chicks which were still gaining weight at fledging). Once fed chicks reached optimal weights, they presumably could allocate more energy to other aspects of development (i.e. feather growth) before fledging.

Chick survival

Fledging success exhibited the greatest response to supplemental feeding of all the variables studied. Indeed, supplemental food all but eliminated the commonly observed difference in survival between *a*- and *b*-chicks. In contrast, food supplementation did not dramatically increase the survival of fed *a*-chicks over unfed *a*-chicks. Thus, *b*-chick survival appears to the more sensitive indicator of food supply. A combination of *a*-chick resource domination, slower growth rates and decreased parental attendance probably led to lower survival rates in unfed *b*-chicks.

Chick begging and feeding rates

Observational studies of Kittiwakes indicate that when local feeding conditions are poor, begging is heightened and feeding rates decline (Wanless & Harris 1992, Roberts & Hatch 1993). However, in this study, with the exception of single chicks, food supplementation did not significantly change the frequency of begging, and chick provisioning rates appeared to be a weak indicator of food supply.

Conceivably, the lack of a response of parental feeding to supplemental food reflects a predetermined level of parental effort (e.g. determined by age) that is independent of foraging conditions (Ricklefs *et al.* 1987, Weimerskirch *et al.* 1997). Low attendance by unfed adults indicated that they had increased their foraging time in an attempt to keep food provisioning constant in poor feeding conditions. However, the slow growth rates and lower

survival of *b*-chicks indicate that unfed parents could not provide sufficient food to meet the demands of both chicks.

Food requirements of *a*-chicks were met first, regardless of food supplementation, because feeding rates of both fed and unfed *a*-chicks were higher than those of their younger siblings. Despite similar rates of provisioning by parents, the quantity of food consumed by unfed chicks ultimately was much smaller than that of fed chicks, because the latter increased their intake via the feeding trays (= 15 days after hatching). It is also possible that fed chicks received larger amounts of food during each delivery from their parents, a factor we could not quantify.

Sibling aggression

Previous studies of Kittiwakes have found a negative relationship between food and the level of sibling aggression (Braun & Hunt 1983, Irons 1992, Roberts & Hatch 1993). However, fed and unfed *a*-chicks directed similar rates of aggression toward their younger nest mates. This indicates that brood reduction at unfed sites was primarily the result of resource domination by the *a*-chick (and thus *b*-chick starvation) rather than direct siblicide. Nevertheless, sibling aggression during late chick rearing ranked 20th in sensitivity to food supplementation, and our inability to detect a relationship between food supply and sibling aggression statistically may be related to the coarse level (i.e. 5-min occurrence intervals) at which the data were collected.

Sensitivity index for breeding parameters

Although many of the breeding parameters we measured were significantly improved by supplemental feeding, that outcome alone provides no indication of their relative usefulness as bio-indicators. The food sensitivity rankings determined in this study appear to be the first such attempt to evaluate the relative importance of many previously used measures simultaneously. Our study suggests that breeding success (specifically fledging success, hatching success and overall productivity), followed by adult time budgets (incubation shifts and attendance during chick rearing) and chick growth parameters (especially for the *b*-chick) are key variables for evaluating annual feeding conditions in Kittiwakes.

Our ranking of breeding parameters as food stress indicators may have considerable generality. However, the way seabirds forage (e.g. surface feeders vs. divers) and the relative sizes of their foraging areas

will influence their responses to fluctuating food supplies (Baird 1990, Hatch & Hatch 1990, Monaghan 1996). In addition, every colony has individual characteristics (e.g. size, habitat and predation pressure) that may alter the relationships between food and any or all of the breeding parameters we studied (Cairns 1987, Regehr & Montevecchi 1997). Nevertheless, our study provides information on which measures might prove most indicative of natural food supply, and may allow researchers to devise better study designs when logistic and time constraints limit observations at a seabird colony. In the future, a supplemental feeding approach that includes adult time budgets and other measures of breeding performance in diving species is desirable to complement this study.

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APPENDIX 1

Parameters observed at three stages of breeding in Black-legged Kittiwakes with predicted and observed outcomes of supplemental feeding.

Stage	Parameter	Prediction	Outcome	Prediction confirmed?	Response to feeding[a]
Prelaying & egg production	Copulation	None	Fed < unfed, 1 interval, 1997	–	Weak
	Courtship begging	Ambiguous	Unfed > fed, 1997	–	Weak
	Courtship feeding	Ambiguous	Fed > unfed, 1 interval, 1996	–	Strong
	Adult attendance	Fed > unfed	Fed < unfed, 1997	No, reversed	Moderate
	Laying date	Fed < unfed	Fed < unfed	Yes	Strong
	Laying success	Fed > unfed	Fed > unfed, 1997	Yes	Moderate
	Clutch size	Fed > unfed	Fed > unfed, 1997	Yes	Moderate
	Egg size	Fed > unfed	Fed > < unfed (*b*-eggs, singles)	Ambiguous	Moderate
	Laying asynchrony	Fed < unfed	Fed ≈ unfed	No	Weak
Incubation	Mean shift length	Fed < unfed	Fed < unfed	Yes	Strong
	Incubation period	No effect	Fed ≈ unfed	Yes	Weak
	Hatching success	Fed > unfed	Fed > unfed	Yes	Strong
	Hatching asynchrony	Fed < unfed	Fed ≈ unfed	No	Moderate
Chick-rearing	Begging rate	Fed < unfed	Fed < unfed, late stage	Yes	Strong
	Feeding rate, early	Fed > unfed	Fed > unfed, early stage	Yes	Moderate
	Feeding rate, late	Ambiguous	Fed > < unfed	–	Weak
	Growth rate	Fed > unfed	Fed > unfed	Yes	Strong
	Sibling aggression	Fed < unfed	Fed ≈ unfed	No	Weak
	Adult attendance	Fed > unfed	Fed > unfed, day 15–40	Yes	Strong
	Fledging period	Ambiguous	Fed ≈ unfed	–	Weak
	Mass at fledging	Fed > unfed	Fed > unfed, 1996	Yes	Moderate
	Fledging success	Fed > unfed	Fed > unfed	Yes	Strong
All season	Productivity	Fed > unfed	Fed > unfed	Yes	Strong

[a]Categories corresponding to percentile rankings of mean effect sizes (absolute values) in Appendix 2 – weak (lowest third), moderate (middle third), strong (upper third).

APPENDIX 2

Sensitivity of kittiwake breeding parameters to supplemental feeding on Middleton Island, 1996–1997.

Breeding stage	Parameter	Response variable	Effect size (sd's)[a]			Rank[b]
			1996	1997	Mean	
Pre-laying & egg production	Courtship begging	Day −19 to −11	0.04	–	0.04	63
		Day −10 to 0	1.03	−0.58	−0.12	50
		Day 1 to 7	0.71	−0.46	−0.13	59
	Courtship feeding	Day −19 to −11	−0.29	–	−0.29	46
		Day −10 to 0	1.89	0.18	1.04	15
		Day 1 to 7	0.43	−0.37	0.03	64
	Copulation	Day −19 to −11	0.48	–	0.48	33
		Day −10 to 0	−0.09	−0.36	−0.23	49
		Day 1 to 7	–	−0.21	−0.21	53
	Attendance	Day −19 to −11	−0.17	–	−0.17	55
		Day −10 to 0	−0.08	−0.97	−0.53	30
		Day 1 to 7	−0.33	−0.60	−0.47	34
	Chronology	Mean laying date	−0.60	−1.16	−0.88	18
	Clutch size	Mean clutch size	0.23	0.41	0.32	44
	Egg volume	*a*-egg	–	0.21	0.21	52
		b-egg	–	0.86	0.86	22
		Single egg	–	−0.92	−0.92	17
		All eggs	−0.08	0.22	0.07	61

APPENDIX 2 *Continued*

Breeding stage	Parameter	Response variable	Effect size (sd's)[a]			
			1996	1997	Mean	Rank[b]
	Asynchrony	Laying asynchrony	−0.15	−0.21	−0.18	54
	Success	Laying success	−0.43	1.65	0.61	26
Incubation	Shift length	Mean duration	4.14	−	4.14	4
	Incubation period	Mean duration	0.16	0.28	0.22	51
	Chronology	Mean hatching date	−0.57	−1.08	−0.83	25
	Asynchrony	Hatching asynchrony	−0.73	0.03	−0.35	41
	Success	Hatching success	2.65	5.90	4.28	3
Chick rearing	Hatching weight[c]	a-chick	0.09	0.12	0.11	60
		b-chick	0.08	0.47	0.28	47
		All chicks	0.08	0.25	0.17	56
	Growth[c]	a-chick (g/day)	0.97	1.26	1.12	14
		b-chick (g/day)	0.92	1.82	1.37	8
		a-chick, peak weight	1.17	0.68	0.93	16
		b-chick, peak weight	1.32	0.97	1.15	12
		a-chick, age peak weight	−0.26	−0.49	−0.38	39
		b-chick, age peak weight	0.12	−0.38	−0.13	57
		a-chick, mass at fledging	1.48	0.26	0.87	21
		b-chick, mass at fledging	1.33	0.35	0.84	24
		a-chick, age at fledging	−0.40	−0.32	−0.36	40
		b-chick, age at fledging	−0.48	0.22	−0.13	58
		All chicks, age at fledging	−0.43	−0.23	−0.33	43
		a-chick, wing chord	−	0.57	0.57	28
		b-chick, wing chord	−	0.85	0.85	23
	Chick begging	a-chick, day 0−20	−	0.55	0.55	29
		b-chick, day 0−20	−	0.38	0.38	38
		Single chick, day 0−20	−	0.00	0.00	65
		a-chick, day 21−40	−	−1.14	−1.14	13
		b-chick, day 21−40	−	−0.88	−0.88	19
		Single chick, day 21−40	−	−1.57	−1.57	6
	Chick feeding	a-chick, day 0−20	0.42	0.34	0.38	37
		b-chick, day 0−20	0.68	0.35	0.52	32
		Single chick, day 0−20	0.30	0.86	0.58	27
		a-chick, day 21−40	−	0.51	0.51	31
		b-chick, day 21−40	−	−0.06	−0.06	62
		Single chick, day 21−40	1.71	−0.84	0.44	36
	Sibling aggression	a-chick, day 0−20	−	0.29	0.29	45
		b-chick, day 0−20	−	−0.34	−0.34	42
		a-chick, day 21−40	−	−0.87	−0.87	20
		b-chick, day 21−40	−	−0.45	−0.45	35
	Adult attendance	Day 0−14	−	0.24	0.24	48
		Day 15−40	−	1.49	1.49	7
	Fledging success	a-chicks	3.16	1.70	2.43	5
		b-chicks	7.60	8.85	8.23	1
		Single chicks	2.19	0.40	1.30	9
		All chicks	6.98	5.83	6.41	2
All season	Productivity	Fledglings/site with pair	1.01	1.37	1.19	11
		Fledglings/nest with eggs	1.12	1.37	1.25	10

[a]Effect size is the response of breeding parameters to supplemental feeding expressed in standard deviations: $(x_{fed} − x_{unfed})/sd_{unfed}$. Expected sign of effects (+ or −) indicated in Appendix 1.
[b]Mean effect sizes ranked by their absolute values. Numerically small ranks indicate variables strongly affected by supplemental feeding.
[c]Single chicks combined with a-chicks because no differences were detected between groups.

APPENDIX 3

Growth parameters of Black-legged Kittiwake chicks in relation to feeding treatment and hatching sequence on Middleton Island, 1996–97.[a]

Year	Treatment	Hatching order	Mass at hatching (g)	Weight gain (g/day)[b]	Peak mass (g)	Age at peak mass (days)	Wing growth (mm/day)[c]	Mass at fledging (g)	Age at fledging (days)
1996	Fed	a-chick	37.7 ± 1.4 (21)	16.8 ± 0.4 (21)	466.7 ± 6.4 (21)	30.2 ± 0.7 (21)	–	424.4 ± 6.2 (11)	41.4 ± 0.5 (16)
		b-chick	34.9 ± 1.1 (16)	15.9 ± 0.5 (13)	442.9 ± 5.3 (12)	29.4 ± 1.1 (12)	–	405.1 ± 9.4 (7)	41.2 ± 0.6 (9)
	Unfed	a-chick	37.2 ± 0.7 (74)	14.5 ± 0.3 (61)	417.1 ± 5.6 (58)	31.4 ± 0.6 (58)	–	374.7 ± 5.0 (45)	42.4 ± 0.4 (33)
		b-chick	34.5 ± 0.6 (55)	11.6 ± 0.9 (25)	364.4 ± 13.7 (19)	28.8 ± 1.1 (19)	–	341.4 ± 15.1 (10)	42.9 ± 1.3 (7)
1997	Fed	a-chick	35.2 ± 0.7 (21)	16.1 ± 0.4 (19)	427.7 ± 8.1 (18)	30.7 ± 0.8 (18)	7.5 ± 0.1 (9)	380.7 ± 10.4 (15)	42.9 ± 0.7 (13)
		b-chick	34.9 ± 1.0 (11)	15.7 ± 0.6 (9)	420.2 ± 13.0 (9)	31.9 ± 1.0 (9)	7.5 ± 0.1 (9)	386.0 ± 11.8 (9)	43.3 ± 0.9 (6)
	Unfed	a-chick	34.9 ± 0.4 (66)	13.2 ± 0.3 (53)	401.4 ± 5.6 (47)	32.9 ± 0.6 (47)	7.2 ± 0.1 (52)	369.1 ± 6.8 (42)	43.8 ± 0.5 (29)
		b-chick	33.6 ± 0.5 (41)	11.0 ± 0.6 (19)	365.8 ± 16.1 (12)	34.6 ± 2.0 (12)	6.3 ± 0.3 18	372.1 ± 12.7 (10)	42.7 ± 1.8 (3)

[a]Values in table are mean ± se; sample sizes (*n* of chicks) in parentheses. Single-chick broods pooled with *a*-chicks because no differences were detected in the parameters measured.
[b]Measurements taken when chicks were 5–25 days old.
[c]Measurements (wing chord) taken when chicks were 10–30 days old; not measured in 1996.

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